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ADDITIONAL REMARKS ON WING STRUCTURE IN *TRACTOCERUS*

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In a recent article published in the BULLETIN, King (1955) advances the hypothesis that "the ancestor of the genus *Atractocerus* diverged from that of the remainder of the Coleoptera after the development of elytra and before the formation of the usually accepted suborders." Accordingly, he proposes to remove the genus from the Lymexylonidae and to place it in a separate suborder of Coleoptera, the Aplicalae.

King's hypothesis rests on two conclusions, neither of which seems justified to me. These are (1) that the wing of *Atractocerus* retains a vein (Cu_{1b}) not present in the wings of other Coleoptera and (2) that the absence of transverse folding in the wing of *Atractocerus* is a primitive feature retained from a common ancestor of the Megaloptera and Coleoptera. In a note published shortly after the appearance of King's article Forbes (1956) points out that the distribution of furrows at the base of the wing indicates that King's identification of Cu_{1b} in *Atractocerus* is erroneous. However, Forbes does not discuss the absence of folding or certain other venational peculiarities of the wing of the genus which have some bearing on the problem of determining venational homologies.

Rather than enter into a detailed discussion of King's argument myself, I propose to demonstrate that the wing of *Atractocerus*, with all its peculiar features, may be easily derived from that of a typical lymexylonid by means of a number of specialized steps most of which have been duplicated elsewhere in the Coleoptera, and particularly in the Rhipiphoridae.

The derivation suggested is shown in figures 1 to 7, beginning with the wing of a species of *Melittomma*, proceeding through several hypo-

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thetical intermediate stages, and ending with the wing of *Atractocerus brasiliensis*. Needless to say, it is extremely unlikely that the steps postulated actually occurred in the order shown. Many of them are evident in the figures of the wings of representative genera of Rhipiphoridae given in my paper on *Nephirtes* (Selander, 1957). The venational nomenclature used for *Melittomma* follows that of King except that his $1A_1$ is labeled $1A_2$ in keeping with Forbes' (1922) interpretation that the first branch of this vein has been lost in the Lymexylonidae and a number of other Polyphaga. It should be noted that in both Forbes (1922) and my *Nephirtes* paper the vein labeled Cu_2 in the present paper is called $1A$, and the vein labeled $1A$ is called $2A$, etc.

Step 1 (fig. 2). *The first radial crossvein ($1r$) is lost, and the remnant of the radial recurrent vein ($2r+R_s$) aligns with crossvein $r-m$.* This specialization has occurred several times in the evolution of the Polyphaga. For example, the radial cell is eliminated in some Pyrochroidae, Anthicidae, Rhipiphoridae, Tenebrionidae (Forbes, 1922, fig. 50), and Dryopidae (Forbes, 1922, fig. 41), and in all Meloidae. In most instances the radial recurrent vein retains its longitudinal position and projects as a free tip basad of crossvein $r-m$. This is not the case, however, in the species of *Melittomma* shown in figure 1. Various degrees of alignment of the radial recurrent vein and $r-m$ are seen in the Meloidae. Nearly perfect alignment is attained in some species of this family and in the genera of Rhipidiinae in the Rhipiphoridae.

Step 2 (fig. 3). *The part of media (M) basad of its connection with crossvein $r-m$ (i.e., the free part of the median recurrent vein) is lost.* In *Atractocerus*, then, the transverse vein interpreted by King as $r-m$ is actually a serial vein formed by this crossvein and a short length each of R_s and media. A close approach to this condition is found in many Meloidae, and Forbes' (1922) illustrations show that the free tip of media is quite short in representatives of several other families of beetles.

Step 3 (fig. 4). *The basal connection of Cu_2 with Cu_1 is broken, and Cu_2 attaches to the base of $1A$.* Under King's interpretation also the venational fork produced in step 3 is regarded as of secondary origin. The basal connection of Cu_1 and Cu_2 is weak in many beetles, including *Melittomma*, and is broken in some others (e.g., several Rhipiphoridae).

Step 4 (fig. 5). *The base of $1A_2$ is lost.* Vein $1A_2$ now appears to arise as a branch of Cu_2 , to which it is connected by crossvein $cu-a$. Again, this specialization is paralleled in some Meloidae (*Eletica*) and Rhipiphoridae (*Pelecotoma*, *Toposcopus*). An intermediate step, in which $1A_2$ is only narrowly broken from $1A$, is seen in *Melittomma sericea* Harris

as well as in some Melandryidae and Mycetophagidae (Forbes, 1922, figs. 45, 53) and a few Rhipiphoridae.

Step 5 (fig. 6). *Cell 1A is eliminated by complete fusion of vein $1A_3$ with $2A_1$.* This leaves a swelling at the middle of vein $1A_3+2A_1$. Essentially the same specialization has taken place within the family Rhipiphoridae and is the general rule in the Meloidae.

Steps 6 to 11 (fig. 7). *The costal vein is extended to the apex of the wing. Vein M_4+Cu_1 is straightened. The discal cell is narrowed. The shape of the wing is modified. The transverse vein and the fork Cu_2-1A_2 migrate basad. Strong convexity of venation is developed.* All but the last two steps are duplicated or closely paralleled in the wings of the rhipidiine Rhipiphoridae. All appear to be intimately related specializations, serving to increase the rigidity of the wing and to otherwise adapt it for powerful flight. The resulting wing, with its triangular form and fanlike arrangement of heavy, straight, well-spaced veins, is not much different basically from the wings of such rapid-flying insects as the Sphingidae, Aegeriidae, and in particular the aberrant mayfly *Lachlania* (fig. 8; see also Edmunds, 1951).

Barber (1952) describes *Atractocerus* as a rapid and powerful flyer and correctly interprets the significance of the modified venation and form of its wings. Barber also calls attention to the reduced, essentially rudimentary condition of the elytra in *Atractocerus*, an aspect of its morphology whose importance King overlooks. Brachelytry itself is not particularly unusual in Coleoptera, but it is a pertinent observation that specializations of wing venation, many of which parallel those in *Atractocerus*, are particularly common (although by no means universal) among beetles with shortened elytra, including members of the Cantharidae, Phengodidae, Teleguesidae, certain groups of Cerambycidae (e.g., Necydalini) and Rhipiphoridae (Rhipiphorinae and Rhipidiinae), and the Stylopidae.

The explanation of this correlation seems evident enough. The more or less complex system of folds in the apical region of the hind wings of most beetles and the interrupted venational pattern which facilitates this folding are adaptations surely developed concomitantly with the evolutionary modification of the fore wings to form elytra. By protecting the hind wings and the dorsum of the abdomen the elytra evidently conferred a great advantage on the first beetles; indeed some authors would ascribe the phenomenal success of the order Coleoptera in large part to the possession of elytra. However, this advantage was gained at the expense of mobility. Thus not only have the fore wings lost much or all their value in flight, they probably are outright hindrances

to rapid movement. Similarly, the hind wings in developing folding have become less efficient as organs of flight.

From this it follows that should a selective premium be placed on rapid, powerful flight (or on some other specialized flight ability), there would be strong selection for reduction or loss of the elytra. This seems to have been the case in *Atractocerus* and many other brachelytrous beetles showing deviation from the normal pattern of wing folding and interrupted venation. In others, such as the Cantharidae and Cerambycidae, whose wings retain the folding specializations intact or nearly so, this explanation is not satisfactory. Presumably in these cases reduction of the elytra serves mainly or entirely the purpose of exposing the membranous hind wings for mimetic effect.

Interestingly, in the Rhipiphoridae, Teleguesidae, Stylopidae, Phengodidae, and *Atractocerus* the surface area of either the antennae or the palpi has been greatly enlarged in the male, which presumably enhances the sensory function of these organs. In the Phengodidae, Stylopidae, and some Rhipiphoridae, and possibly in the Teleguesidae the female is wingless, and in these groups it would appear that the increased efficiency of sensory perception and flight of the males compensates for the general immobility and secretiveness of the females. This does not hold true for *Atractocerus*, however, where the females show the same specializations as the males in the characters under consideration. Perhaps in this genus low population density or some peculiarity of dispersal or courtship has placed a premium on ability to orient on prospective mates and to fly with great rapidity. Other lymexylonids have the maxillary palpi as highly modified as in *Atractocerus*, but none has developed the specialized flight of the genus.

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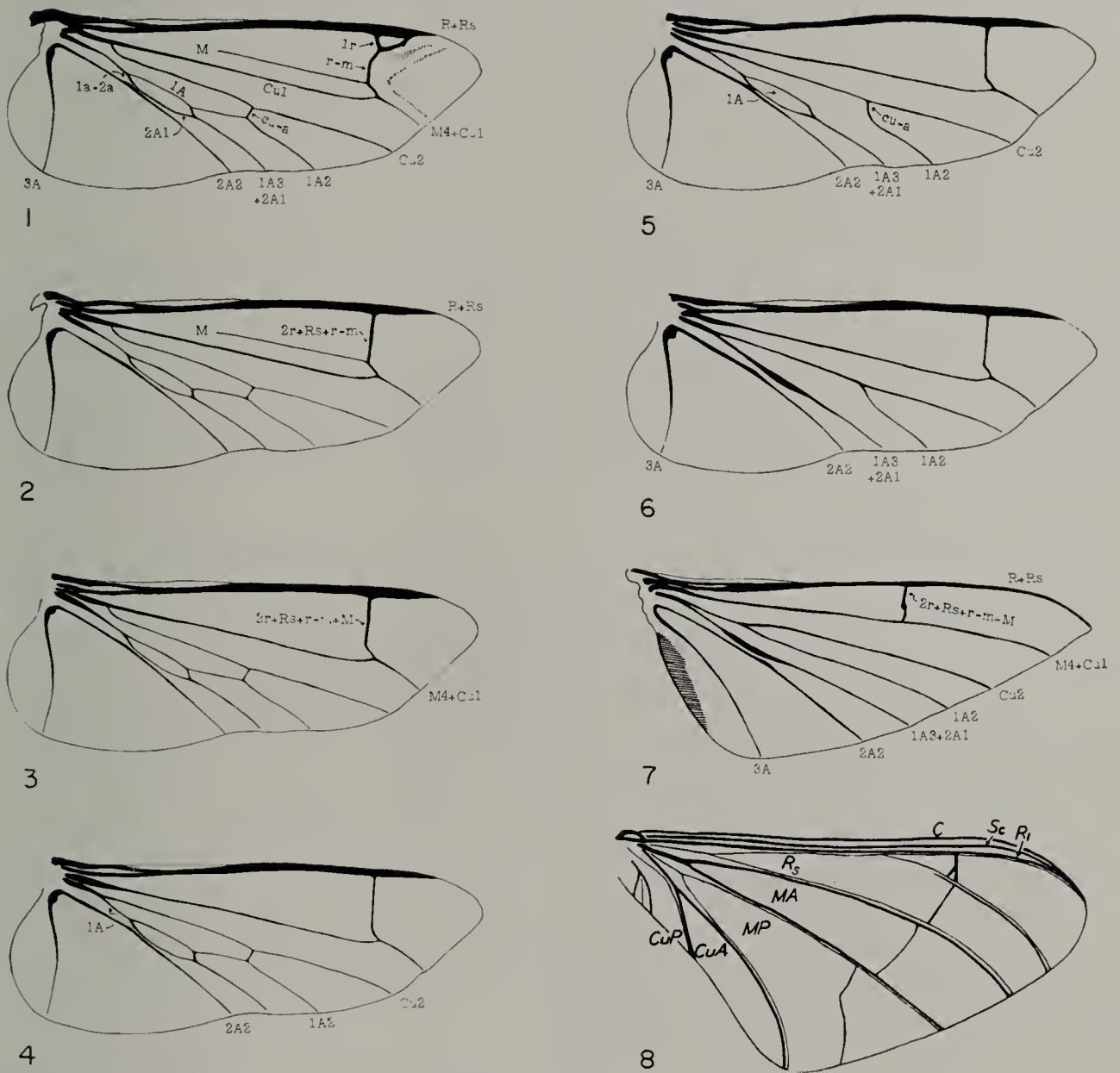


FIGURE 1. *Melittomma* sp. (Mexico), wing. FIGURES 2-6. Hypothetical stages in the evolution of the wing of *Atractocerus*. FIGURE 7. *Atractocerus brasiliensis* Lepelletier & Serville, wing. FIGURE 8. *Lachlania powelli* Edmunds (Ephemeroptera), fore wing (after Edmunds, 1951).